

Biology of the range crane fly, *Tipula simplex* Doane

(Diptera: Tipulidae)

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The range crane fly, *Tipula simplex*, described by Doane (1901), is a univoltine pest of valued rangeland in the San Joaquin Valley. The larvae live in the grass of unirrigated pastures and when at high density, will eat the grass roots. Tulare County reported outbreaks of the species in 1961, 1967, and 1973. This latest outbreak affected 800 hectares on one ranch alone, with a crane fly density of 3000 larvae per square meter. At this high density, the crane fly larvae denude the hills of all grass and other forage, with an adverse effect on the watershed. However, such high densities of crane flies occur only occasionally and ranchers detect no signs of the larvae in intervening years. Since little information on the biology of the species has been reported, this study was undertaken to determine the species' life history and habits, as necessary prerequisites to understanding the causes of the population fluctuations. This study was conducted on unirrigated pasturelands in the foothills of the Sierra Nevada mountains in northern Tulare County from October, 1974 through March, 1976, and was supplemented with laboratory rearings and experiments.

Habitat

In May the soil starts to dry out and by the end of June the soil contains only 0.3% water by weight. By mid summer the soil moisture has dropped to 0.2% with the temperature one inch below the surface of the soil exceeding 50° Celsius during the day. The first rain usually comes in September (about 1/2 inch), stimulating the growth of turkey mullein or dove weed (*Eremocarpus setigeras* Benth.), vinegar weed or bluecurls (*Trichostema lanceolatum* Benth.), and tarweed (*Hemizonia congesta* DC.), but the soil dries out almost completely before the second rains come (usually in October). After these second rains the forage crops appear, and the soil remains moistened by periodic rain until April when the rains end, and the soil starts drying out again.

Adults and Oviposition

The males usually emerge before the females in February or March. When the female adult emerges the male grasps her and sometimes

pulls her out of her pupal case. Copulation occurs immediately, and in the laboratory will continue for 24 hours. When the female is released, she walks and pulls her way through grasses in the field until she falls into a depression in the ground. These depressions may be holes caused by loosened clods of soil and rocks, or imprints of cattle hooves. The female will oviposit all her eggs (average 96, $S = 28.6$) in the soil together, approximately $\frac{1}{2}$ and $\frac{3}{4}$ inches below the surface. Neither male nor female have been seen feeding. All adults in any one field emerge within a three week period.

Eggs

The egg is the stage which must survive the harsh summer conditions of high temperature and low moisture.

In the laboratory we were able to induce hatching by drying the eggs for six months at a 16:8 photoperiod, then transferring them to a 10:14 photoperiod. They were kept moist for two weeks, then dry for one week, and then moist again. The hatching rate was 5.2% within one week. Hatching could be induced by this procedure anytime in the fall, but not if the alternate wettings and dryings were started in January or later. However, an additional 5% would hatch at age 18 to 21 months old, if the above mentioned wetting and drying regimen was repeated in September of the second year after oviposition.

Eggs are laid in clumps, which makes sampling difficult. Lang (unpublished data) collected 13 samples (11.5 diameter circle, to a depth of $\frac{3}{4}$ inch). From each sample he took 4 samples of 5 grams each for testing. The number of eggs per 5 gram sample ranged from 0 to 2641, with a mean of 68.48 ($S = 174.43$). Obviously, sampling for eggs would require a large number of samples to insure that the sample mean is similar to the population mean. Hanson's equation (1967) allows us to calculate the number of samples necessary to approximate the population mean ($n = t^2 se^2 / (\bar{x} - \mu)^2$, where n is the number of samples, t is the student T statistics for whatever confidence level, $s.e.$ is the standard error, $(\bar{x} - \mu)$ is the amount of deviation from the true population mean that the investigator will accept. Using Lang's data, and calculating 95% confidence limits, we can calculate that we must take 48 samples to be 95% sure that the sample mean is within 10% of the true population mean, or 195 samples to be 95% sure that the sample mean is within 5% of the true population mean.

Larvae

The first instar has never been found in the field. Laboratory rearing of eggs to hatching indicate that the first instar is morphologically different from the other three instars. The second instar larvae show a clumped distribution due to the oviposition habits of the females. By the time the crane flies are third instar larvae, a different pattern of

aggregation is observed. The crane flies are spread evenly throughout the grass, but are highly aggregated under cowpads that are one or more seasons old, under pieces of wood, or under any other debris in the field. For example, in one field, cowpads had 1104 individuals/meter² ($S = 513.3$) while in the grass the density was 193 individuals/meter² ($S = 32.9$). The degree of aggregation in part depends upon the dryness of the field. In the very dry winter of 1976 virtually all the crane flies in the field were concentrated under cowpads (2200 larvae/meter²).

The fourth instar larvae retain the aggregated pattern. However, during the late fourth instar (January and February) predation by birds takes a heavy toll. The birds that are most often seen eating the crane fly larvae are blackbirds and starlings, although curlews and meadow-larks will also feed on the larvae in years of high crane fly density. The most typical mode of feeding is for the birds to flip over one year old cowpads and feed on the larvae underneath (curlews) or poke their beaks through the cowpad and eat both the larvae which have burrowed into the manure and those which live between the cowpad and the soil (starlings and blackbirds). This predation drastically changes the distribution pattern. The remaining aggregations are located under and around older cowpads which have grasses growing through them, making them less vulnerable to predation by birds.

Predation ceases abruptly with pupation of the larvae. When birds turn over a cowpad which has both larvae and pupae under it, they feed only on the larvae.

Pupae

In one week, the percentage of crane flies in the pupal stage rises dramatically (12% to 82%). Males and females can be easily distinguished at this stage (Hynes and Hartman, in preparation). The pupae make movements in response to light and pressure, but have limited locomotion. The pupal stage is fairly short. The first adults appeared in the field 12 days after the first pupae.

Aggregation

The aggregation pattern of early second instar larvae is believed to be due to the habit of adult females laying all their eggs in the same place.

The second, third, and fourth instar larvae are much more motile than the first instar, and it is not surprising that a change in the distribution pattern occurs. Laboratory tests were performed in 1974 and 1975 to determine the factors influencing the habitat choice of the older larvae.

The test apparatus was a straight tube (30 x 25 x 4 cm) which was divided into two equal halves. Different conditions could be maintained in each side of the tube. Parameters tested were light (0 versus

5.6 lux) and moisture (0 versus 2 gm water on 12.5 cm diameter filter paper). Tests, when both sides of the cage had identical conditions, indicated that the larvae showed no preference for either side of the cage. When animals were given a choice between a moist and a dry environment, they always spent a significantly greater amount of time in the moist environment. The response to light was more variable. If both sides of the cage were moist the animals spent a significantly greater period of time in the dark. If both sides of the cage were dry, the animals exhibited no preference for light or dark, and moved continually (Table 1).

This indicated a kinesis in response to water. Further tests on speed of movement indicated that a larva in a moist artificial environment moved at a rate of 0.08 cm/sec and in a dry artificial environment it moved at a rate of 0.16 cm/sec. This was significant using the paired difference test. In a moist environment the number of headturns that a larva made in a given time was not significantly different than the number of headturns for the same period of time when the animal was in a dry environment. By definition (Denny and Ratner, 1970), the larvae show an orthohydrokinetic response, that is they slow down, but do not increase turning, in the presence of soil moisture.

The response to light was also tested by putting the crane fly larvae into a more natural condition of soil or manure in a cage. Their response to light above and below them was tested. All larvae moved down as light was shined from above (6 tests, 4 larvae/test) and 27 out of 32 larvae moved upward as light was shined from below (8 tests, 4 larvae/test). The difference between the numbers of larvae moving up to escape light versus the numbers of larvae moving down to escape light was not significant (Student's t test). These results indicate that the crane fly larvae are negatively phototactic, and that their response to light overrides any response to gravity.

Table 1. Preference for Conditions of Moisture and Light

Test	# of larvae tested	Conditions in preferred side of maze (A) and mean minutes spent	Conditions in non-preferred side of maze (B) and mean minutes spent	Mean difference in time spent in two sides A-B
5	5	dry/dark (19)	dry/light (11)	8 min N.S.
6	5	wet/dark (25.2)	wet/light (4.8)	20.4**
7	5	wet/dark (27.4)	dry/dark (2.6)	24.8**
8	5	wet/light (26.2)	dry/light (3.8)	22.4**
9	5	wet/light (24.6)	dry/dark (5.4)	19.2**
10	5	wet/dark (25.8)	dry/light (4.2)	21.6**

** $p > .01$

Finally, we performed a test to determine if a substance produced by the crane fly larvae affected aggregation. Ten larvae were placed in a cage containing moist filter paper (9 cm diameter) for 24 hours, on which they defecated and left skin traces. This paper containing the excretions of the larvae and moist filter paper were placed in a large cage (9 x 10 x 100 cm) containing a layer of moist sand. A number of fourth instar larvae were then introduced into the cage. After 24 hours, it was found that 94% of the larvae were collected under the filter paper with crane fly extract and 6% were found under the control paper. The aggregation index (Roth and Cohen, 1973) for this crane fly substance is 0.875. (1 is a perfect aggregation).

We hypothesize that aggregation of third and fourth instar larvae in the field under cowpads or rotten wood is due to the following factors. The area under the cowpads provides a temperate, moist, dark habitat. When larvae wander into the area, they slow down (orthohydrokinesis). The aggregation pheromone acts either to attract other larvae to this favorable environment, or by decreasing the rate of locomotion helps to retard emigration by larvae that have moved into the area by chance.

Distribution

Tipula simplex has a known distribution from northern Santa Cruz County north to Marin County, and across to Sacramento (Alexander, 1967). Another population occurs in Tulare County. The area between Sacramento and Tulare counties may contain the fly, but it has not been recorded in the literature or found by us in this area. In southern Tulare County the proportion of *Tipula simplex* decreases and the proportion of *Tipula acuta* Doane increases. In Kern County (south of Tulare), *Tipula acuta* replaces *Tipula simplex*.

The distribution in fields varies from year to year. In three years we have mapped the areas of crane fly populations on one ranch. In 1974, populations of medium density (100-300 larvae/m²) were found in three fields, LB, SC, and WM and in 1975, very light densities (<50 larvae/m²) were found in the north facing slopes of LCA. In 1976, light densities were found in WM, and medium densities were found in the south facing slopes of LCA, SC, and LC. As a general rule, the same area did not have measureable populations for two consecutive years (an extensive search did not reveal any *Tipula simplex* larvae). One exception to this was field LCA, but the same area was not infested in the two consecutive years.

Density Measurements

We have made several attempts to accurately measure the crane fly larval density. The most successful, to date (our estimated mean is calculated within 6.8% of the true population mean at the 95% confidence limits), involves measuring the number of larvae under 25 cow-

pads of measured size, the number of larvae in 25 samples of grass of similar size, and then estimating the cowpad coverage (which was determined by the point-centered quarter method) (Cottam & Curtis, 1956). In field LC in 1976, for example, the mean of 25 samples was equivalent to 159.7 larvae/meter² cowpads (accuracy 6.8%), 273.3 larvae/meter² grass (accuracy 6.8%) and the cowpad coverage was 1.05% (accuracy 6.2%). The estimated average number of larvae/meter² was 272.1, and we are 95% confident that the actual population mean was between 253.6 and 290.6 larvae/meter² (based on method of Hanson, 1967). Because this sampling was done after bird predation, the mean density of crane flies under cowpads is lower than the mean density of crane flies in grass.

Acknowledgments

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SCIENTIFIC NOTE

Aphilanthops hispidus as a Predator on Bees (Hymenoptera: Sphecidae).—The genus *Aphilanthops* includes only four species, two of them known to prey upon queen bees of the *Formica fusca* group (Evans, 1962, Behaviour, 19: 239-260). It has been assumed that specificity for queen *Formica* ants distinguished *Aphilanthops* ethologically from the related genera *Clypeadon* (prey: worker *Pogonomyrmex* ants) and *Philanthus* (prey: bees and wasps). However, *Aphilanthops hispidus* Fox, a deserticolous species of southwestern U.S. and northwestern Mexico, is a predator on bees. I located a nest of this species on 12 June 1975, 16 km W of LaPaz, Baja California Sur. The female was seen bringing bees into a burrow in coarse, flat sand in an arroyo, and the nest was excavated. I failed to find any cells, but I did find 7 paralyzed bees stored in the burrow 30 cm from the entrance, 12 cm below the surface. They belonged to 4 different families: *Colletes daleae* Cockerell (3♂♂) (Colletidae), *Agapostemon melliventris* Cresson (1♂), *A. mexicanus* Robertson (1♂) (Halictidae), *Ashmeadiella meliloti* Cockerell (1♀) (Megachilidae), and *Epeolus* sp. (1♀) (Anthophoridae). I am indebted to Dr. R. M. Bohart for identifying the wasp and to Dr. G. C. Eickwort for identifying the bees. — **HOWARD E. EVANS**, Department of Zoology and Entomology, Colorado State University, Fort Collins, CO 80523.